

## Dispatches

# Eco-Evolutionary Dynamics: Community Consequences of (Mal)Adaptation

Contemporary evolution can shape ecological dynamics at population, community and ecosystem levels. Innovative new experiments with walking sticks confirm this expectation by showing that adaptation to predatory birds has large effects on walking stick population sizes, arthropod communities and herbivory.

Andrew Hendry

"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us."

Charles Darwin, On the Origin of Species

Ecologists have long sought to disentangle Darwin's bank by considering interactions among species and between species and their environments. For the most part, these efforts have been devoid of evolutionary considerations — except to recognize that different species, and thus their different ecological effects, are the product of past evolution. Instead, ecologists have traditionally assumed that species' characteristics are relatively invariant properties — at least on the time scales relevant to their research [1]. In perhaps the clearest statement of this perspective, Slobodkin [2] codified a difference between "ecological time" and "evolutionary time," with the latter supposedly representing the much longer time periods required for evolution to disrupt ecologically stable states. More recently, this whole perspective — and Slobodkin's caricature of it — has become a straw man for the new view that evolution can be dramatic even on short time scales and can thereby alter ecological processes in real time — a phenomenon called 'eco-evolutionary dynamics'. A new study by Farkas and colleagues [3] in this issue of *Current Biology* fires the latest — and

perhaps most powerful — salvo in this sea-change.

Darwin famously stated that evolution by natural selection must be very slow: "we see nothing of these slow changes in progress, until the hand of time has marked the long lapses of ages" and "she can never take a leap, but must always advance by the shortest and slowest steps." Despite a few early examples of apparently rapid evolution, most famously in peppered moths, this view of evolution as a sedate process prevailed for at least a century. Soon after Slobodkin's assertion [2], however, a growing number of studies began to show that noteworthy evolution could occur over only decades. Evidence of this so-called 'rapid' or 'contemporary' evolution has continued to accumulate until, at present, so many concrete examples exist that essentially everyone acknowledges the convergence of ecological and evolutionary time [4–7]. With this acceptance has come the impetus and incentive to investigate how contemporary evolution influences ecological processes — that is, as we contemplate it.

Several studies have confirmed that contemporary evolution can alter ecological dynamics at the population, community, and ecosystem levels [8–16]. However, each of these studies has been limited in one or more respects, such as a lack of experimental manipulations (leaving causation unclear) or the use of artificial arenas (leaving relevance to nature unclear). The new study by Farkas and colleagues [3] removes these limitations and thereby provides one of the clearest examples of the importance of evolutionary change for ecological dynamics.

*Timema cristinae* walking sticks are flightless insects that inhabit the southwestern United States. They live, feed, and mate on their host plant, with common host plant species including *Ceanothus spinosus*, which has broad ovate leaves, and *Adenostoma fasciculatum*, which has fascicled needle-like leaves. Over the past 12 years, Patrik Nosil and colleagues have shown that *Timema* occupying these two host plants are differentially adapted and show reduced gene flow consistent with the onset of speciation — that is, they qualify as 'host races' [17]. The most striking adaptive difference between the races is their different colour patterns (presence versus absence of a dorsal stripe), which make them camouflaged on their respective host plants to visually hunting birds, such as scrub jays [18]. Importantly, however, the level of adaptation varies among *Timema* populations (Figure 1) as a function of dispersal (movement of walking sticks between host plants) and founder effects (random evolutionary changes that can occur when only a few individuals establish a new population). Specifically, camouflage of the *Timema* population on a given host plant can be compromised by high dispersal or recent colonization from the 'wrong' host plant [19]. This variation in the level of (mal)adaptation would turn out to be critical for demonstrating eco-evolutionary effects.

Farkas and colleagues used the *Timema* system to test for the ecological effects of (mal)adaptation in camouflage. Without any prior data to draw on, they first experimentally manipulated the level of (mal) adaptation to see if the extremes could influence ecological variables. The experiment started by moving *Timema* with different color patterns (with or without the dorsal stripe) among different host plants to generate situations where adaptation was very strong (most *Timema* were camouflaged) or very weak (few

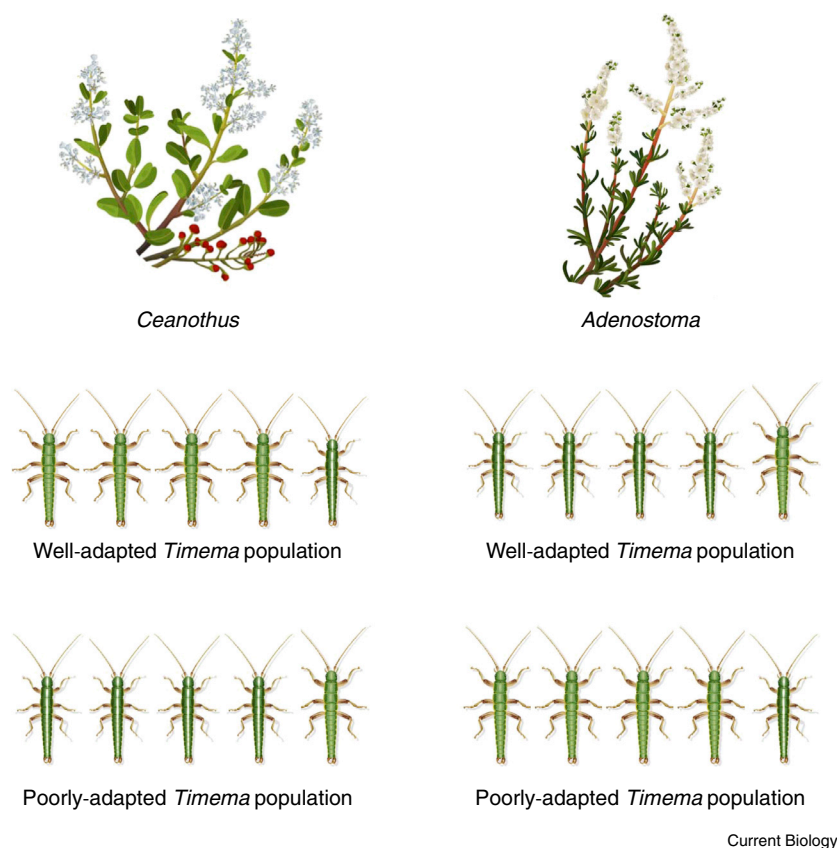


Figure 1. Adaptation of *Timema* walking sticks to different host plants.

On *Ceanothus* host plants (left column), *Timema* walking sticks without a dorsal stripe are well adapted (camouflaged in the face of bird predation); whereas, on *Adenostoma* (right column), *Timema* with a dorsal stripe are well adapted. The degree of local adaptation of *Timema* populations on individual host plants can vary from strong (high frequency of the locally-camouflaged color pattern) to weak (low frequency of the locally-camouflaged color pattern). Drawings by Rosa Ribas.

*Timema* were camouflaged), along with intermediate conditions. One month after these manipulations, the authors returned to the study site and exhaustively sampled all of the arthropods on each experimental plant. The results were encouraging: *Timema* in experimental populations that were better adapted (better camouflaged) at the start of the experiment were more abundant a month later, confirming that (mal)adaptation had a causal influence on population dynamics.

Although experimental manipulations are important for demonstrating causation, they can leave uncertain the relevance to natural situations — that is, in the absence of experimental manipulations. What was needed, then, was a complementary study relating natural variation in *Timema* (mal)adaptation to natural variation in ecological parameters. This

effort was accomplished through an intensive mapping study of *Timema* populations in a 35 x 63 m area that included 117 individual *Adenostoma* plants and 69 individual *Ceanothus* plants. The authors mapped the location and size of each plant and then caught and scored the coloration of all *Timema*. Echoing the experimental manipulation, natural variation in *Timema* (mal)adaptation was closely related to *Timema* population size. Moreover, this association was about as strong as the association between traditional ecological drivers (plant species and plant size) and *Timema* population size. Finally, an eco-evolutionary model [20] that included the effects of dispersal and adaptation fit the real data quite well. Reassuringly, then, effects demonstrated in the experimental manipulation were also clear — and

strong — in unmanipulated populations.

What about consequences beyond population dynamics: that is, do the effects of *Timema* (mal)adaptation cascade to community-level processes? Returning to the experimental manipulation, the authors found that better-adapted *Timema* populations at the start of the experiment led to more abundant and more diverse arthropod communities at the end of the experiment. This effect was quite strong and somewhat surprising. *Timema* are competitors of a number of other arthropod species; so why would greater *Timema* maladaptation that decreases *Timema* population size lead to fewer other arthropods? The authors [3] suggest the effect might arise through shared predation. Maybe poorly-adapted *Timema* populations attracted more birds — a reasonable hypothesis given that (mal)adaptation was based on camouflage — which then eat more of the other arthropods too. Testing this hypothesis became the goal of a second field season. The experiment was similar to the manipulation performed previously, but this time enclosures were placed around some of the plants to keep birds out. This experiment yielded the same result — increased maladaptation leads to fewer *Timema* and fewer other arthropods — but only when the cages were absent and birds were therefore present. This new experiment thus established the specific causal force — predatory birds — behind eco-evolutionary dynamics at the population and community levels.

A final question was whether eco-evolutionary effects could cascade all the way to ecosystem-level parameters? To gain some initial insight into this question, Farkas and colleagues [3] examined herbivory on the host plants and found that, as might be expected, herbivory by sap-feeding insects decreased as arthropods became rarer as a result of increased maladaptation by *Timema*. Thus, the authors had experimentally-confirmed effects of (mal)adaptation in nature at the population, community, and ecosystem levels (Figure 2). Of course, much work remains to be done, including a determination of the specific effects of birds (i.e., consumptive or non-consumptive), a formal demonstration of the relative

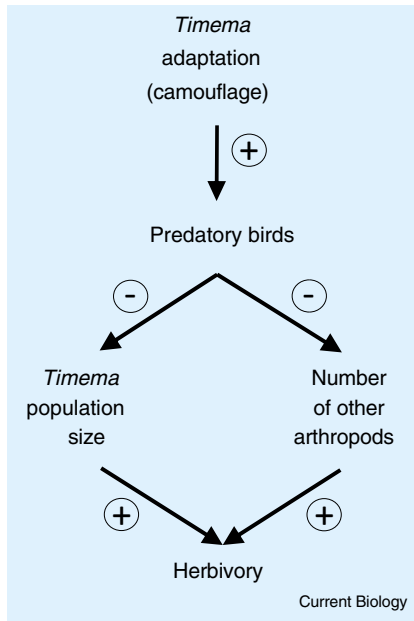


Figure 2. Eco-evolutionary effects discovered by Farkas *et al.* [3].

Reduced adaptation (camouflage) by *Timema* walking sticks (Figure 1) leads to more predatory birds, which leads to fewer *Timema* and fewer other arthropods, both of which result in decreased herbivory (which route is most important has yet to be determined). Feedbacks not illustrated here are also likely, such as that from predation on *Timema* adaptation and from *Timema* population size to both predation and *Timema* adaptation.

contribution of *Timema* and other arthropods to herbivory, a test for various feedbacks (some possibilities are noted in the caption to Figure 2), a consideration of the effects of *Timema* evolution across generations, and an examination of additional

ecosystem-level variables (e.g., productivity, decomposition, nutrient cycling).

The elegant demonstration of eco-evolutionary effects — and their surprising strength — in the *Timema* system will hopefully encourage other investigators to look at well-established ecological systems for evidence of evolutionary effects and at well-established evolutionary systems for evidence of ecological effects. Only thus can we hope to disentangle Darwin's bank.

#### References

1. Strauss, S.Y., Lau, J.A., Schoener, T.W., and Tiffin, P. (2008). Evolution in ecological field experiments: implications for effect size. *Ecol. Lett.* 11, 199–207.
2. Slobodkin, L.B. (1961). *Growth and Regulation of Animal Populations* (New York: Holt, Rinehart and Winston).
3. Farkas, T.E., Mononen, T., Comeault, A.A., Hanski, I., and Nosil, P. (2013). Evolution of camouflage drives rapid ecological change in an insect community. *Curr. Biol.* 23, 1835–1843.
4. Hendry, A.P., and Kinnison, M.T. (1999). The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53, 1637–1653.
5. Stockwell, C.A., Hendry, A.P., and Kinnison, M.T. (2003). Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* 18, 94–101.
6. Hendry, A.P., Farrugia, T.J., and Kinnison, M.T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* 17, 20–29.
7. Reznick, D.N., and Ghalambor, C.K. (2001). The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112–113, 183–198.
8. Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N., and Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.* 11, 609–623.
9. Bailey, J.K., Schweitzer, J.A., Ubeda, F., Koricheva, J., LeRoy, C.J., Madritch, M.D., Rehill, B.J., Bangert, R.K., Fischer, D.G., Allan, G.J., and Whitham, T.G. (2009). From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Phil. Trans. Roy. Soc. B: Biol. Sci.* 364, 1607–1616.
10. Post, D.M., and Palkovacs, E.P. (2009). Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Phil. Trans. Roy. Soc. B: Biol. Sci.* 364, 1629–1640.
11. Saccheri, I., and Hanski, I. (2006). Natural selection and population dynamics. *Trends Ecol. Evol.* 21, 341–347.
12. Kinnison, M.T., and Hairston, N.G., Jr. (2007). Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Func. Ecol.* 21, 444–454.
13. Pelletier, F., Garant, D., and Hendry, A.P. (2009). Eco-evolutionary dynamics. *Phil. Trans. Roy. Soc. B: Biol. Sci.* 364, 1483–1489.
14. Schoener, T.W. (2011). The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429.
15. Bassar, R.D., Marshall, M.C., López-Sepulcre, A., Zandonà, E., Auer, S.K., Travis, J., Pringle, C.M., Flecker, A.S., Thomas, S.A., Fraser, D.F., and Reznick, D.N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proc. Natl. Acad. Sci. USA* 107, 3616–3621.
16. Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B., and Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* 458, 1167–1170.
17. Nosil, P. (2007). Divergent host plant adaptation and reproductive isolation between ecotypes of *Timema cristinae* walking sticks. *Am. Nat.* 169, 151–162.
18. Nosil, P., and Crespi, B.J. (2006). Experimental evidence that predation promotes divergence in adaptive radiation. *Proc. Natl. Acad. Sci. USA* 103, 9090–9095.
19. Bolnick, D.I., and Nosil, P. (2007). Natural selection in populations subject to a migration load. *Evolution* 61, 2229–2243.
20. Hanski, I., Mononen, T., and Ovaskainen, O. (2011). Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. *Am. Nat.* 177, 29–43.

Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke St. W, Montreal, QC H3A 0C4 Canada.  
E-mail: [andrew.hendry@mcgill.ca](mailto:andrew.hendry@mcgill.ca)

<http://dx.doi.org/10.1016/j.cub.2013.08.023>

## Cellular Aging: Symmetry Evades Senescence

Cellular aging programs typically rely on the asymmetric shape and growth pattern of cells. A new study shows that symmetric fission yeast cells escape classic signs of aging until they encounter environmental stress.

James B. Moseley

It will happen to the best of us. As we age, our bodies slow down and prepare for an inevitable meeting with the grim reaper. The phenomenon of aging has long fascinated biologists: what are the

mechanisms that drive senescence, and how might they be controlled? A defined aging program occurs not only in complex organisms, but also at the level of single cells. Replicative life span refers to the finite number of times a single cell can generate offspring.

Over 50 years ago, Mortimer and Johnston used the budding yeast *Saccharomyces cerevisiae* to show that a 'mother' cell generates about 25 newborn 'daughter' cells [1]. At this point, cell growth slows dramatically and is followed by death. The asymmetric growth pattern of budding yeast cells is key to this aging program because it permits the selective retention of 'aging factors' in the older mother cell. These factors include extra-chromosomal rDNA circles and damaged proteins, which have subsequently been shown to contribute to cellular aging in many